

The University of Chicago

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A PART OF A DISSERTATION SUBMITTED TO
THE FACULTY OF THE DIVISION OF THE
PHYSICAL SCIENCES IN CANDIDACY FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF GEOLOGY AND PALEONTOLOGY

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Ernest Paul Du Bois

With the increasing interest of vertebrate paleontologists in the group of "mammal-like reptiles" it has become evident that there is further need of detailed morphologic studies of the related group. With this in mind, a series of studies aimed at a comprehensive description of the skull of *Cnemidophorus* was initiated. It is proposed at a later date to publish data on the soft parts of the head.

Cnemidophorus was chosen because of its generalized structure, its availability, and its small size, which permits the making of serial sections. Two species, *C. gularis* and *C. sexlineatus*, were used.

Acknowledgments for assistance in this study are due to Mr. Karl P. Schmidt of the Field Museum of Natural History, and to Dr. Everett C. Olson and Mrs. Sylvia Bensley, both of the University of Chicago.

Detailed Analysis of the Bones

Frontal.—The frontal is an unpaired bone which extends from the posterior level of the orbits to a point slightly anterior of their forward limits. In cross section the dorsal surface is essentially flat anteriorly, slightly convex between the orbits, and somewhat concave posteriorly. Ornamentation is absent except on the hinder part which is slightly rugose. Anteriorly, the frontal is produced into three processes of about equal prominence. The middle process is inserted between the paired nasals, and the lateral ones between the nasals and prefrontals on each side. Posteriorly, the frontal meets the parietal in a prominent suture. The postero-lateral boundaries are wing-like and are clasped for a considerable distance by the postorbitals. From the ventral aspect, the frontal is flat posteriorly but arched upward anteriorly to allow the passage of the olfactory tracts.

Parietal.—The parietal is an unpaired bone, wider than long, extending from the frontal to the occipital region. The main body of the bone is rectangular, produced antero-laterally into a pair of small wings which articulate with the frontal and postorbital, and postero-laterally into a pair of elongate processes which meet the squamosal and the paroccipital process of the oto-occipital. A small median notch exists in the rear border of the parietal. This notch is commonly closed by a sheet of connective tissue in which is imbedded a small cartilaginous element, possibly the homologue of the dermal-supra-occipital of other forms, or the remainder of the chondrocranial tectum synoticum. The posterior border of the parietal is flanged. Laterally, it is deflected downward over most of its length, forming a pair of lateral plates which partially enclose the sides of the brain. Anteriorly, these plates are some-

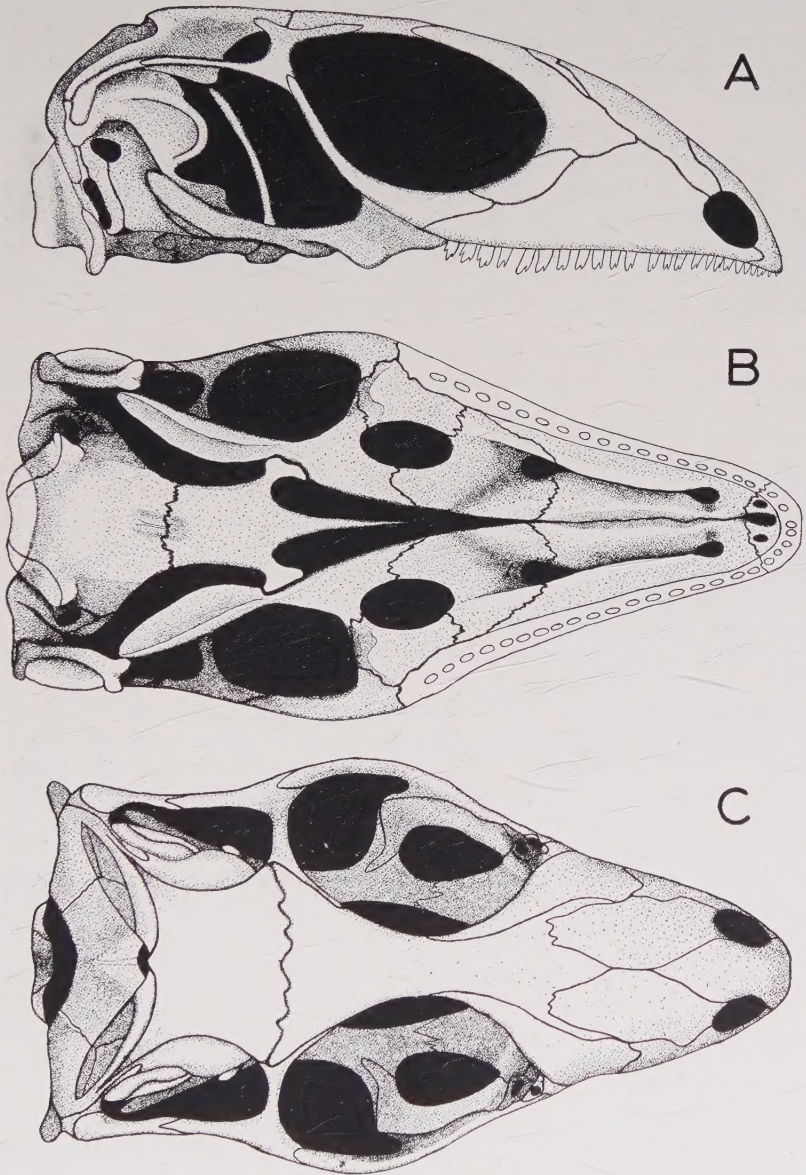


Fig. 1. Diagram ($\times 9$) of skull of *Cnemidophorus* sp. showing (A) lateral, (B) ventral, and (C) dorsal aspects.

what more pronounced and receive the epipterygoids in a pair of poorly developed notches. A median ridge is present on the ventral side of the parietal, partially filling in the cerebral fissure. The entire dorsal surface is more or less rugose.

Supraoccipital.—The supraoccipital is a large median element lying between the parietal and the foramen magnum. It is united ventro-laterally with the oto-occipital and laterally with the proötic by well developed sutures. A poorly defined median ridge divides the supraoccipital into right and left halves. The posterior end of the anterior semi-circular canal and the medial end of the posterior semi-circular canal unite in the supraoccipital to form the crus communis. Their courses may be easily seen through the thin covering of bone.

Oto-occipital (*Parotic* and *paroccipital* of authors).—The oto-occipital bounds the foramen magnum laterally. It consists of the fused exoccipital and opisthotic. Traces of the sutures between these bones persist. The ventral portion of the posterior semi-circular canal is largely confined to the opisthotic but seems to enter into the exoccipital to an indeterminable extent. Laterally, the paroccipital process articulates by means of a cartilaginous element with the quadrate below and with the squamosal anteriorly. It meets a very attenuated portion of the parietal dorsally. The suture separating the oto-occipital from the proötic starts at the junction of the suture between the supraoccipital and oto-occipital with that between the supraoccipital and the proötic. It proceeds from this point postero-laterally to the union of the parietal arch and the paroccipital process, and then proceeds ventrally to the fenestra ovalis in front of the fenestra rotunda and finally terminates in an unossified zone between the basioccipital, opisthotic, and proötic. From this unossified zone, the suture dividing the basioccipital and oto-occipital may be traced posteriorly for a short distance. It then turns dorsally and terminates at the posterior border of the fenestra rotunda. The oto-occipital forms the ventral and posterior border of this opening. From the posterior border of the fenestra, the line of union swings around the basioccipital tubera and then medially across the back of the skull to the foramen magnum. The twelfth nerve exits by two openings in the exoccipital portion. The condyle is single and tripartite, the exoccipital forming its dorso-lateral portions.

Basioccipital.—The basioccipital forms the lower border of the foramen magnum and extends anteriorly to the basisphenoid. It is bounded laterally by the oto-occipitals and proötics. The antero-lateral margins are clasped by a pair of processes extending back from the basisphenoid. Near its posterior margin, the basioccipital exhibits a pair of strongly developed ventral processes, the basioccipital tubera, which extend laterally and posteriorly. A slight median ridge extends back from the basioccipital-basisphenoid suture for a distance equivalent to one-third of the length of the bone.

Basisphenoid.—The basisphenoid extends anteriorly from an irregular suture which separates it from the basioccipital. The basipterygoid processes are well developed and expanded distally at their junction with the pterygoids.

The parasphenoid¹ rostrum is membranous and easily lost during preparation. It extends far forward between the pterygoids and palatines. The sella turcica is pronounced as a result of the well developed dorsum sellae which forms its posterior wall. A slender process of the proötic lies alongside the basisphenoid and is suturally related to its lateral edges.

Proötic.—The proötics form the lateral walls of the brain case. Their structure and relationships are complex. Each proötic is divided by a well developed ridge which starts at the parietal arch and proceeds antero-ventrally to the proximal end of the basipterygoid process. Anterior to this ridge the proötic consists of a vertical plate, in which lies most of the anterior semi-circular canal, and which articulates dorsally with the parietal and posteriorly with the supraoccipital and oto-occipital. Posterior to the ridge, the proötic is also plate-like but is oriented in a somewhat different plane. The posterior edge forms the border of the fenestra ovalis. Ventrally the proötic meets the basioccipital and basisphenoid.

Quadrate.—The quadrate lies ventral to the distal end of the paroccipital process from which it is separated by a cartilaginous pad. Each quadrate consists of a slightly recurved bony axis with a pair of wings on the lateral and medial sides so shaped that they, particularly the lateral one, resemble backward-facing cups. The lateral wing is considerably larger than the medial. The inner portion of the distal end of the quadrate is connected by means of a cartilaginous pad to the outer surface of the pterygoid. The distal end of the otostapes lies posterior to the main axis of the quadrate, to which it is bound by connective tissue.

Pterygoid.—The pterygoid extends from the ventral surface of the quadrate anteriorly to join the palatine with which there is sutural union. In general, the pterygoid is Y-shaped and consists of the quadrate process, posterior, and the palatine and ectopterygoid processes, anterior. A cartilaginous pad exists between the pterygoid and ectopterygoid. The quadrate process is flat but bears on its ventral surface a knife-like ridge which extends from the level of the basisphenoid union posteriorly to the end of the bone. The basipterygoid process fits into an oblique groove on the pterygoid. The meniscus pterygoideus is present and moderately developed. The epipterygoid arises from a depression on the dorsal surface at about the same level as the union with the basisphenoid. Three palatal teeth are present medially near the anterior end of each pterygoid.

Ectopterygoid.—The ectopterygoid lies antero-laterally to the pterygoid process of the pterygoid. It articulates with four bones: postero-medially with the pterygoid, postero-laterally with the jugal, antero-laterally with the maxil-

¹ Much confusion is present in the literature as to whether the process directed anteriorly from the basisphenoid is pre- or parasphenoid, some authors going so far as to use the terms synonymously. Their separate identity is easily established embryologically by their different antecedents and morphologically by the presence of both bones in many reptiles. The parasphenoidal identity of this process may be established embryologically, structurally, and paleontologically.

lary, and antero-medially with the palatines. An oval infra-orbital fossa is enclosed between the pterygoid, ectopterygoid, and palatine.

Epipterygoid.—The epipterygoid has been treated incidentally to the description of other bones. It is a rod-shaped structure extending from the pterygoid, in which it fits into a groove, to the parietal, in which it is received in a poorly defined notch.

Palatine.—The palatine extends anteriorly from the pterygoid to the vomer. Laterally, for a short distance, the palatine meets the ectopterygoid, and for a much longer distance, the alveolar surface of the maxillary. Anteriorly it is united by a suture to the vomer. Strongly developed depressions at the anterior ends of the palatines indicate the openings of the internal nares. The antero-medial edges of the palatines are prevented from meeting in the midline by a pair of posteriorly directed processes from the vomer.

Vomer.—Although in recent years this bone has been known as the "prevomer," in light of the recent researches of Parrington and Westoll,² the use of the early term seems advisable inasmuch as these authors have shown that the reptilian vomer is homologous to the mammalian vomer. The vomer in *Cnemidophorus* is formed of paired lateral members. Posteriorly, it joins the palatines, anteriorly, the maxillary and premaxillary. Small foramina on the antero-lateral edges of the vomer connect the buccal cavity with Jacobson's organ. In the prepared skull these foramina are confluent with the internal nares. There are no vomerine teeth.

Septomaxillary.—The septomaxillary is a thin plate which extends obliquely from the trabecula communis ventrally and laterally beneath the nasal passages to the lateral border of the vomer. It is not visible except in cross section.

Premaxillary.—The premaxillary is a median bone composed of fused lateral members. It articulates ventrally with the vomer, laterally with the maxillaries, and dorsally with the nasals, between which a long nasal process is inserted. Teeth are much reduced on the premaxillary.

Maxillary.—The maxillary forms most of the lateral surface of the anterior part of the skull. It articulates with the nasal, prefrontal, lacrimal, jugal, ectopterygoid, palatine, vomer, and the premaxillary, and forms a part of the border of the external nares. It is excluded from the infra-orbital fossa by the ectopterygoid. Each maxillary bears about 17 teeth which are pleurodont in their mode of attachment. The teeth are generally single-cusped, but frequently have a small subsidiary cusp anteriorly, and less frequently, posteriorly. The teeth are constantly replaced by others coming in at their base. Numerous nutrient foramina are present along the lateral margin of the maxillary.

Jugal.—The jugal is a relatively long curved bone which forms most of the lower margin of the orbit. Anteriorly, it articulates with the lacrimal and the

² F. H. Parrington and T. S. Westoll, "On the Evolution of the Mammalian Palate," Phil. Trans. Roy. Soc. London, Series B, 230:305-355, 1940.

maxillary. Posteriorly, articulation is with the fused postorbital-postfrontal. Ventrally, the jugal meets for a short distance the pterygoid and ectopterygoid.

Squamosal.—The squamosal has simple relationships. It is sliver-like, reaching from the postorbital-postfrontal in front, to the tabular behind. The posterior end is slightly flared. Approximately half of the lower border of the supratemporal fossa is formed by the squamosal.

The identity of the squamosal is related directly to the phylogenetic history of the lizards. Recent studies on *Youngina*, *Youngoides*, and other pro-lizard types seem to indicate quite clearly the origin of the Lacertilia from a diapsid stock. If this be the case, the only logical identity of the bone in question is squamosal.

Tabular.—The tabular is an elongate bone forming the antero-ventral border of the parietal arch. It is inserted between the squamosal, parietal, and oto-occipital. From this position it proceeds antero-medially along the ventral surface of the posterior process of the parietal.

Postorbital-postfrontal.—In *Cnemidophorus* the postorbital and postfrontal are fused into an X-shaped bone which separates the orbit from the supratemporal fossa. It has two medial processes which clasp the frontal and parietal, and two lateral processes which articulate with the jugal and squamosal.

Prefrontal.—The prefrontal lies, as the name suggests, anterior and lateral to the frontals. It sends a process posteriorly along the medial border of the orbit. The nasals make slight contact with the bone; the maxillaries meet it over most of its anterolateral border. The lacrimal lies lateral to the prefrontal.

Lacrimal.—The lacrimal forms the border of the lower part of the anterior wall of the orbit. It meets the prefrontal dorsally, the jugal ventrally, and the maxillary anteriorly. Inside the orbit, the lacrimal sends a very pronounced plate medially, across the anterior orbital wall, nearly to the midline. This plate extends from the palatine below to the prefrontal above. In the ventro-lateral corner of this plate is the opening for the lacrimal duct.

Nasal.—The nasal extends from the posterior edge of the external naris posteriorly and medially to the frontal. The paired nasals meet in the midline for a short distance, but are separated anteriorly by a process from the premaxillary and posteriorly by a similar process from the frontal. Laterally, union is made with the prefrontal and maxillary.

Stapes.—The stapes is a rod-like bone which extends from the fenestra ovalis laterally to the posterior border of the quadrate. It is slightly swollen at both distal and proximal ends.

Detailed Analysis of the Foramina

Lacrimal.—The foramen through which the lacrimal duct passes is a relatively large opening situated between the medially deflected blade of the prefrontal and the lacrimal bone. The opening is crescent shaped with the

convexity directed laterally. Anteriorly, the maxillary replaces the lacrimal in forming the lateral boundary of the lacrimal canal. There is some indication of the double nature of the lacrimal duct in emarginations present on the dorsal and ventral margins of the crescent.

Infraorbital.—The infraorbital foramen, through which passes the superior alveolar branch of the fifth nerve, lies slightly ventral to the lacrimal foramen. It is bordered dorsally by the inflected portion of the prefrontal, medially by the palatine, and ventrally and laterally by a prolongation of the maxillary. In some cases the ectopterygoid may form a portion of its posterior border. A short distance anteriorly, the medial wall of the canal disappears and the foramen is replaced by a groove in the alveolar portion of the maxillary.

Maxillary.—Normally, five or six maxillary foramina are present on the lateral surface of each maxillary bone. They are arranged in an anterior-posterior row located immediately above the dental margin of that bone. These openings allow small twigs of the superior alveolar branch of the fifth nerve to pass out of the bone laterally and to supply innervation to the glandular tissues in the membranes of the upper lip. Small blood vessels generally accompany these twigs but are more irregular in their presence.

Nasal.—Usually, three small openings on each maxillary and about eight on each nasal indicate the places of exit of small terminal twigs of the rami nasalis medialis and lateralis. The lateralis twigs are restricted to the maxillary and the medialis to the nasal. There seems to be little regularity in the arrangement of these openings.

Proötic incisure.—The proötic incisure, while not strictly a foramen, is a very important landmark. It is located at the inferior-anterior margin of the proötic, immediately ventral to the genu of the anterior semicircular canal. It normally lodges the ganglion of trigeminal nerve.

Abducens.—The sixth nerve passes through a small foramen in the antero-lateral floor of the basisphenoid. The foramen courses forward in the upwardly deflected body of the bone, above the carotid canal, and appears again on the postero-lateral wall of the sella turcica.

Carotid.—The internal carotid artery maintains a ventro-anterior course over the external surface of the proötic bone and, in older specimens particularly, is protected by a projecting superjacent ledge of the proötic. Anteriorly the artery enters the body of the basisphenoid, with the palatine branch of the seventh nerve, at a level near that of the basioccipital-basisphenoid suture, and a short distance posterior to the proximal end of the basipterygoid process. The canal proceeds through the basisphenoid ventral to the abducens canal and enters the posterior wall of the sella turcica somewhat ventral and medial to the opening of the abducens.

Facial.—The root of the facial nerve penetrates the proötic immediately ventral to a larger opening which marks the anterior acoustic foramen. The external opening of the facial lies ventral to the oblique ridge which shelters

the carotid and in life is covered by the ganglion of the seventh nerve. From this ganglion, a palatine branch runs forward paralleling the carotid and entering the basisphenoid through the carotid canal. Within the basisphenoid, the carotid canal gives off a lateral branch through which passes the palatine nerve and a small accompanying blood vessel. The opening for the palatine nerve lies in the angle which the basipterygoid process makes with the basisphenoid.

Acoustic.—The medial aspect of the brain case exhibits several large foramina. Immediately dorsal to the facial foramen is a large opening, the anterior acoustic foramen, which marks the entrance of the anterior branch of the eighth nerve. A deep depression proceeds posteriorly from this opening and terminates in another large foramen, the posterior acoustic. Within this latter opening, in its roof, a minute foramen is present which transmits dorsally a small branch of the posterior auditory nerve.

Endolymphatic.—Some distance above the aforementioned complex lies a foramen through which passes the endolymphatic duct. It is located at the apex of a triangular boss, the base of which is marked by the foramina acustica and facialis.

Rotunda and Cochleae.—Ventral and posterior to the acoustic complex, a large perilymphatic canal passes out of the cranial cavity. Its outer opening, the fenestra rotunda, is covered by the secondary tympanic membrane. Dorsally, a well developed fenestra cochleae enters the perilymphatic canal and connects it with the vestibule of the ear. Externally, the fenestra rotunda is an elliptical opening immediately ventral to the fenestra ovalis and separated from it by a narrow blade of bone. The fenestra rotunda lies between the opisthotic and proötic.

Ovalis.—The fenestra ovalis is a more or less elliptical opening which lies dorsal to the fenestra rotunda. It is bordered along most of its dorsal, posterior, and ventral margin by the opisthotic and along its anterior margin by the proötic.

Hypoglossal.—Ventral and posterior to the fenestra cochleae, within the brain case, three small openings mark the passage of the several roots of the hypoglossal nerve. Externally, the roots of the hypoglossal are indicated by two small foramina lateral to the occipital condyle and ventral to the jugular foramen.

Jugular.—The jugular foramen is a large opening which lies above the external openings for the hypoglossal nerve. Within the brain case it lies posterior to the hypoglossal foramen.

Pineal.—The pineal body has no external opening but is lodged in a depression on the ventral side of the parietal.

